

XLVIII.—On Spontaneous Division in the Echinodermata and other Radiata. By Dr. C. F. LÜTKEN.

[Concluded from p. 337.]

DALYELL* and Semper† have investigated the faculty of regeneration in the Holothurida; and the former has established that a voluntary spontaneous division really takes place at least in some species of those Echinoderms. It is to be regretted that with regard to the faculty of regeneration and to artificial division we do not yet possess any methodical observations upon other Echinoderms, especially the Asterida and Ophiurida, in which the frequent cases of regeneration which have been observed lead us to deduce the possibility of artificial division if it were tried. But even if this were the case it would not prevent our interpreting the phenomena already described as a natural or spontaneous binary or radial division, seeing that we are not in a position to discover an exterior influence capable of exerting upon the life of these animals so profound and singular an action, but we can only seek the cause of these natural phenomena of division in an act emanating from the organism itself and having *multiplication* for its object.

Like the authors who have treated before me of heteractinism in the Ophiurida and Asterida, I must therefore hold to the hypothesis that in the cases already specially examined (*Ophiothela*, *Ophiactis* (p. p.), *Ophiocoma* (p. p.), *Asterias* (p. p.), *Linckia* (p. p.), and *Ophidiaster* (p. p.)) it is due to a true *spontaneous* division, no doubt repeated several times. But, as I have already pointed out, however acceptable this explanation may appear, it cannot be regarded as the true one until it has been verified upon animals kept alive for a long time in aquaria. Nevertheless it has so many probabilities in its favour that it is well to call attention to it—especially at a time when “experimental zoology” already possesses a review of its own, and the establishment of zoological stations is being realized on the shores of that very sea which harbours two of the species in which we suppose such a division to occur, namely *Ophiactis virens* and *Asterias tenuispina*. If we could succeed in keeping these species alive for a long time in aquaria, it would no doubt be easy to settle the following points—namely, whether a natural division really takes place, whether it is repeated several times, whether it ceases when the animals attain a certain age or size and when the organs have acquired a certain degree of development, &c. These phenomena possess

* Powers of the Creator, vol. i. pp. 49 *et seqq.*

† Reisen im Archipel der Philippinen, 2ter Theil, Band i. p. 201.

a special interest, because the Holothurida, Asterida, and Ophiurida are the highest organisms in their sphere in which a true spontaneous division has been ascertained or supposed to occur; and as other forms of agamic reproduction, *e. g.* gemmation, are entirely unknown in the class Echinodermata*, there is the less reason here than elsewhere to regard division as a disguised gemmation or something of the kind. Spontaneous division, therefore, is manifested in this class of animals with exceptional purity and independence. If we suppose that it is really a division that takes place here, it is a division pure and simple, and not a mask under which something else is hidden (gemmation or some analogous mode of multiplication).

In fact, although spontaneous division has always been represented as a special category of the various modes of reproduction of the lower animals, especially as a subdivision of agamic reproduction, and although the text-books assign to this mode of reproduction a comparatively wide domain, it is evident that in many cases the spontaneous division is only apparent; in reality it is often something quite different that takes place; and the part ascribed to this mode of reproduction is thus so much reduced that it is easy to understand how doubts may have arisen whether natural spontaneous division ever takes place, with the exception, of course, of the animals placed at the very bottom of the scale (Rhizopoda, Monera), in which the notions of cell and individual are almost confounded, and the individual, with the other properties of the cell, has also inherited its divisibility. Thus, in many Infusoria, a "division in the direction of the length" has been supposed in cases in which there was only a copulation; two individuals have been found half united and half free, and it has been concluded that they were in course of separation, while, on the contrary, they were engaged in the no less astonishing operation of fusing into one†.

* In publishing a very interesting observation upon viviparity in an Echinid (*Anochanus*), M. Grube (Monatsb. Akad. Wiss. Berl. 1868, p. 178) has put forward the hypothesis that it was a case of agamic reproduction by means of germs or internal buds; but in reality there is no sufficient reason for accepting this supposition, nor do I see how the difficulties presented by the history of the reproduction of that Echinid can be diminished by it. M. Grube's hypothesis, moreover, is connected with the theory according to which the formation of the Asterid or Echinid in the *Pluteus*-larva is not a metamorphosis, but a gemmation—an opinion the incorrectness of which I thought zoologists had long since recognized.

† Besides this operation, which is the opposite of a division, there is produced apparently in these animals a true longitudinal division of the various bell-animalcules, which enables them to form colonies, when one of the two newly formed bells does not detach itself. But it remains to be learned whether this division, as in other Infusoria, is not in reality a disguised production of two perfectly new individuals.

The transverse division of the Infusoria also is not a true division. As M. Steenstrup has indicated, it results clearly from the beautiful observations of M. Stein that it is not an individual that divides into two, but two young individuals that are developed in the same mother and become free by absorbing her body. We must also join with those naturalists (Boeck, Steenstrup) who maintain, as resulting clearly from observation, that the act by which the *Scyphistoma* becomes transformed into the *Strobila* (by multiple transverse scission), and the latter breaks up into a series of young *Medusæ*, is only a slightly disguised development of a series of internal germs or buds, accompanied by an absorption of the Medusa-nurse (the *Scyphistoma*), exactly as in the Infusoria, with the sole difference that the number of germs is much greater than in the latter.

We may also doubt whether a true spontaneous division ever takes place among the Vermes (at all events those of the highest rank); it would seem that in most cases it is only a disguised gemmation. To discuss this question thoroughly with regard to the fissiparous Chætopoda (Naïdes, Syllidea, Tubicola) would carry me far beyond the limits of this memoir, and would nevertheless throw no light upon the subject; it will suffice for me to remind the reader that whilst it seems to result positively from some observations that what takes place here is a gemmation, or a successive development of a series of germs or buds in the posterior extremity of the worm, many observers regard it as beyond doubt that there is a pure division followed by a regeneration of the part separated. These questions being in general surrounded by a certain obscurity, observers have probably in most cases not been fully conscious of the distinction to be established, and consequently have not overcome its difficulties. However, as it cannot be doubted that it is always the same phenomenon that takes place here, *i. e.* either a true division or a true gemmation, the balance in opinion inclines strongly to the latter side. It seems to me that the observations we possess may be readily brought into accordance with the opinion that the so-called scissiparity of the Chætopoda is only a disguised terminal gemmation, precisely as in the Medusa-nurses.

That the faculty of regeneration is extremely great in the Vermes is a well-known fact. In certain cases, as O. F. Müller showed a hundred years ago (by very exact experiments, in which spontaneous division with the regeneration resulting from it is most distinctly separated from natural scissiparity or gemmation), it attains such a development that artificial division is produced with great facility. In the present day

we possess interesting observations by Mr. MacIntosh, showing that certain Nemertina (*Borlasia*) when in confinement may break up into a quantity of fragments, all of which possess the power of regeneration so as to become complete individuals. This kind of division, which is neither entirely spontaneous nor entirely artificial, is difficult to range under any definite scientific determination; we find analogous cases among the Actiniæ.

Spontaneous division (schizogony) seems therefore to occur principally in two great groups of the lower animals:—the *Protozoa* (Monera and Rhizopoda), which are reduced to simple cells, and which consequently may be divided artificially and divide themselves; and the *Radiata* (Echinoderms and Cœlenterata), in which the divisibility is partly connected in a perfectly natural manner with the radiate structure. But both in the Echinodermata and in the Cœlenterata spontaneous division is at the same time intimately connected with regeneration, upon which it depends, and from which it cannot be separated: we may regard it as the most perfect expression of its development; and in some Cœlenterata (especially the Actiniæ) it is moreover in intimate connexion with gemmation (blastogony), and passes so insensibly into perfectly characterized phenomena of gemmation, that, at any rate in a great many cases, it seems impossible to trace a boundary between these two modes of reproduction, which seem to be so essentially different. As the experiments made upon this subject have never been considered in their totality, and it would be very desirable that they should be resumed in a methodical manner, I have appended to my communications on spontaneous division in the Echinodermata a short statement of what has been ascertained as to regeneration and artificial and natural division in the Medusæ and Actiniæ. By this means I propose to collect some materials which may assist in answering the following questions:—Of what facts which may throw light upon the spontaneous division of certain Radiata is science in possession? and in what relation does spontaneous division stand on the one hand to artificial division, and on the other to gemmation and other forms of agamic reproduction?

With regard to the Medusæ, I leave on one side the so-called scissiparous division of the *Scyphistoma*, and also pass over in silence the celebrated observations on the spontaneous and artificial division of the freshwater polypes, as likewise the interesting experiments of M. Häckel on the artificial division of the ova and embryos of the Siphonophora. In fact, in all these cases, as in the researches of Dalyell and Reid on artificial division (both longitudinal and transverse) in the *Scyphi-*

stoma, we have not to do with the division of a true "individual" in the strict acceptation of the term, but with that of a creature which is really very simple, but potentially and *in nuce* is a multiple creature, which would resolve or develop itself into a long series of individuals. I therefore confine myself to references to those cases in which a true artificial or spontaneous division has been observed in the Medusæ—namely, by M. Hæckel in the species of the group *Thaumantias*, and by M. Kölliker in young *Mesonemata* (*Stomobrachium*). If, however, Hæckel's observations relate to Medusæ of the category which Mr. Allman subsequently termed "Gonochemes" this case would have to be assimilated to those which, for reasons explained above, fall outside the considerations here involved. After mentioning the spontaneous and artificial division of *Protohydra*, a type which is still but little known, and also the artificial division of *Lucernaria* and the spontaneous division of *Schizocladium* (which appear to me to have just as much resemblance to gemmation or sporogony), I take up the examination of the faculty of regeneration and the divisibility of the Actiniæ, commencing with the remarkable investigations of Dicquemare, which are already a century old, and then passing in review the more recent experiments and observations of Gosse, Peach, Bennett, Dalyell, M'Cready, Mrs. Thynne, Van Beneden, Wright, and Hogg. From these it appears not only that the Actiniæ may be divided longitudinally and transversely, but also that spontaneous division is by no means a rare phenomenon, at least in some species (*A. cereus*, *dianthus*, *cavernosa*); in an Actinid probably produced from the ova of *Caryophyllia Smithii* it was even repeated so frequently that, in the course of two years, two individuals were thus increased to 278. By a similar longitudinal division the frequent appearance of double Actiniæ more or less joined together has also been explained; but their formation may be interpreted in a different way.

Although in the Actiniæ (except, perhaps, *Corynactis*) gemmation cannot be regarded as a normal mode of reproduction, as in the compound Anthozoa, it nevertheless occurs sometimes in them—partly in the same species which are subject to spontaneous longitudinal division, and (as in the supposed *Caryophyllia Smithii*) in conjunction with this latter operation. Consequently these two modes of agamic reproduction, different as they are in form, evidently replace one another, and cannot differ much in their essence; moreover, when the division is a little excentric, and one of the parts is a little smaller than the other, we may ask ourselves whether the division is not really a disguised gemmation. The limit is no less difficult to

trace in those cases in which small portions of the margin of the pedal disk of the Actiniæ spontaneously, accidentally, or artificially detached acquire an independent life and become developed into Actiniæ (*A. lacerata*, *dianthus*). Spontaneous transverse scissiparity is known only in *Gonactinia (prolifera)*; and even this has much more the character of a gemmation.

The faculty of regeneration is likewise highly developed in the Fungia; and in consequence of injuries it often happens that an individual splits into two or more, or that a larger or smaller number of buds are produced; for in these normally simple Anthozoa gemmation is not a normal phenomenon, and it is not always possible to trace a precise boundary between gemmation and the regeneration which takes place after an injury. What has been described in *Diaseris* as a union of several sectors originally separate is rather a spontaneous or semispontaneous division, followed by phenomena of regeneration and gemmation.

Although an important part has been ascribed to spontaneous division in the compound Madreporaria, and it has even been supposed that this mode of multiplication characterizes certain systematic groups, I have become convinced that its importance in this respect is completely illusory, and that it will be found, by a more careful examination, that in most cases (*e. g.* the *Meandrinae*) this supposed division is only a gemmation. As my master, Prof. Steenstrup, pointed out to me many years ago, the new individual always originates as an isolated bud; but as it grows, the boundary between it and its nearest neighbour, which must be regarded as its nurse, is seen gradually to be effaced. This is precisely the opposite of what has been supposed. The individuals (*e. g.* in the *Euphyllia*, the *Mussa*, and the *Symphyllia*) begin by being isolated, and finish by being more or less completely fused into one another. I think, therefore, that the interpretation of these facts given by Mr. Dana approaches nearer to the truth than that of M. Milne-Edwards; and I must maintain that (leaving out of consideration the intercalicinal gemmation, which it would be very difficult to distinguish from division) no true spontaneous division has yet been ascertained to occur in the compound Madreporaria.

The result of the investigations and considerations which have been set forth here, partly *in extenso* and partly in the form of a summary, is as follows:—

If there are many cases in which spontaneous division is only a more or less disguised gemmation, and in which we are not yet in a position to separate clearly one from the other,

there are nevertheless many other cases in which it by no means presents this character, but, as expressed by the term, is a *division* and nothing else. In some cases (in the Asterida and Ophiurida above mentioned, and perhaps in certain Actiniæ) this division is probably a normal form of increase which replaces gemmation; in others, on the contrary, it appears to be quite accidental. On the one side, therefore, it is related to regeneration, on the other to gemmation. Although it is not always possible to indicate clearly the limit between these phenomena, and division and gemmation often replace each other, this does not prevent our retaining for "schizogony" an independent place in the series of modes of agamic multiplication (monogony), side by side with internal and external gemmation (blastogony), and with multiplication by free germs (sporogony) or by unfecundated ova (parthenogony), especially as it is a deduction from the scientific value and importance of these categories that it seems to be difficult or even impossible to trace a marked line of separation between these modes of multiplication, or between parthenogony and sexual reproduction. But, as I have indicated above, the classification in the category of schizogony of the phenomena of multiplication already described in the Asterida and Ophiurida has precisely the effect of clearly establishing that spontaneous division differs qualitatively from gemmation, which might well have been regarded as doubtful so long as we had exclusively or chiefly in view the phenomena presented by the Coralliaria and Actiniæ.

The general propositions which sum up the present state of our knowledge regarding spontaneous division may therefore, I think, be provisionally enunciated as follows:—

1. The most energetic manifestation of the faculty of regeneration in animals is *divisibility*.

2. In certain forms of Radiata in which the faculty of regeneration is highly developed, *spontaneous division* occurs either alone (Asterida and Ophiurida) or associated with gemmation (Actiniæ).

3. True spontaneous division, or *schizogony*, in the Actiniæ, Medusæ, Asterida, and Ophiurida (which must not be confounded with the disguised gemmation of the Infusoria, of *Scyphistoma*, and of certain Chætopods) must be regarded as a peculiar form of agamic reproduction, side by side with blastogony, sporogony, and parthenogony.

*Latin characters of new Species referred to in this Paper.*1. *Ophioderma tongana*.

Granula disci minuta, scutella radialis obtegentia; incisuræ disci scutella dorsalia brachiorum bina vel terna intima amplexæ; scuta oralia latiora quam longa, triangularia, extus rotundata, intus acuminata, angulis lateralibus rotundatis; scutella adoralia granulis obtecta; papillæ orales octonæ, exteriores latæ, obtusæ, interiores acuminatæ, angustæ; scutella ventralia brachiorum octangula, longiora quam lata, lateribus excavatis; dorsalium latitudo longitudinem duplam æquat; spinæ laterales octonæ, depressæ, breves, dense collocatæ, æquales et scutella lateralia dimidia æquant, infima tantum cæteris major. Diam. disci (speciminis juvenilis) 9 mm.; brachia sextuplo longiora.

Hab. ad insulas Tonganas.

2. *Ophiostigma formosa*.

Discus granulis obtusis, cylindricis infra et sparsius supra obtectus, scutis radialibus tamen nudis, conspicuis; scuta oralia æque longa ac lata, rotundata, intus acuminata; scutella adoralia sat magna, extus latiora, fere transversa, intus et extus sese tangentia, scutello ventrali intimo minutissimo modo sejuncta; papillæ orales quaternæ, externa minuta, rudimentali, cæteræ sat magnæ, æquales, obtusæ. Brachia diametrum disci sextuplum longitudine æquantia, gracilia, apicem versus parum decrescentia, depressa, haud moniliformia; scutella ventralia quadrangula, angulis rotundatis lateribusque excavatis, longiora quam lata, inter se haud sejuncta; spinæ laterales ternæ, breves, acutæ, planiusculæ, latitudinem brachii dimidiam æquant; papillæ ambulacrales binæ; scutella dorsalia ovalia, latiora quam longa. Diam. disci $3\frac{1}{2}$ mm.

Hab. in freto Formosæ dicto.

3. *Amphipholis Andree*.

Discus planus, margine acuto, supra insertionem brachiorum parum inciso, squamis minutis, numerosis, planis, solidis, æqualibus, imbricatis tectus; squamæ marginales distinctæ, biseriatae, ventrales dorsalibus haud minores; spinæ vel granula nulla; scuta radialis mediocria, contingentia, apicibus modo squamula singula vel squamulis binis minutis sejuncta; conjuncta figuram ovalem, extus latiore, fere æque latam ac longam formant; scuta oralia minuta formam solitam rhomboideam acutam exhibent; adoralia linearia triangularia, extus scutello brachiorum ventrali minutissimo sejuncta; papillæ orales quaternæ, binæ intermediae maximæ, interdum divisæ. Brachia elongata, gracilia, fortiter decrescentia, filiformia; scutella dorsalia late ovalia, latitudine longitudinem duplam æquante; ventralia pentagona, ad basin brachiorum latiora quam longa, margine aborali recto, lateralibus excavatis; spinæ

laterales ternæ, minutæ, acutæ, articulos spiniferos fere longitudine æquantes; papillæ ambulacrales geminæ. Diam. disci 8 mm.

Hab. ad oras insulæ Javæ.

4. *Amphipholis Kochii*.

Discus planus, margine rotundato, supra insertionem brachiorum in adultis fortiter inciso, squamis minutissimis utrinque tectus, marginalibus nullis; spinæ vel granula nulla; scuta radialia minuta, angusta, introrsum acutiora, parum divergentia, cuneolo squamarum plane disjuncta; scuta oralia rhomboidea, acuta; papillæ orales ternæ, interna infradentalis, externa maxima; brachia mediocriter elongata, versus apicem decrescentia; scutella dorsalia late ovalia, ventralia pentagona, latiora quam longa, margine aborali recto; spinæ laterales ternæ, validæ, obtusæ, compressæ; papillæ ambulacrales binæ. Diam. disci 6-7 mm.

Hab. ad oras Manschuriæ orientales.

5. *Ophiothela isidicola*.

Discus inter brachiorum sex originem profunde incisus, scutis radialibus 12 maximis fere plane obtectus; zonæ interradales angustissimæ granula sparsa gerunt; tubercula majora pauca, rarius spinæ acutæ breviusculæ in parte centrali disci, in angulis externis interscutellaribus et in lateribus disci inter rimas genitales adsunt; superficies ventralis disci et brachiorum cute molli induta; scuta oralia et adoralia haud conspicua, ventralia brachiorum, nec non papillæ ambulacrales desunt; brachia brevia, sæpe inæqualia, diametrum disci duplum longitudine æquantia, supra granulis rotundatis (in junioribus et in parte externa brachiorum fere evanidis) obtecta, serie media tuberculorum majorum scutellorum dorsalium locum tenente; scutella lateralia fortiter carinata spinas gerunt laterales 5 vel 6, breves, asperas, subtus dentatas vel pectinatas, inferiores breviores et crassiores, medias longiores et graciliores, superiores breviores, apicem versus perpaucas, pluries uncinatas. Diam. disci 5 mm.

Hab. in freto Formosæ dicto in *Paraside laxa* socialis.

6. *Ophiothrix galatææ*.

O. brachiis longissimis, deplanatis, spinisque brachialibus brevibus *O. longipedæ* et *O. nereidinæ* aff., scutis radialibus mediocribus, omnino glabris, disco cæterum supra et infra granulis minutis tecto, distinguenda; granula dorsualia dense collocata, obtusa, ventralia sparsiora, graciliora, acutiora; spinæ brachiales 6-7, inferiores brevissimæ, superiores latitudinem brachiorum parum superantes; scutella dorsualia brachiorum trapeziformia. Diam. disci 14 mm.; brachia 15-20plo longiora.

Hab. ad insulas Nicobaricas.